Equivalence of foliar water uptake and stomatal conductance?

Equivalence of foliar water uptake and stomatal conductance?

Oliver Binks[1], Ingrid Coughlin[1], Maurizio Mencuccini[2], Patrick Meir[1,3]

1. Research School of Biology, The Australian National University, Canberra, 2601 ACT, Australia
2. ICREA at CREAF, Barcelona 08010, Spain
3. School of Geosciences, University of Edinburgh, Edinburgh EH9 3FF, UK

Abstract

Foliar water uptake, the uptake of atmospheric water directly into leaves, has been reported to occur in nearly 200 species spanning a wide range of ecosystems distributed globally. Until recently, this flux has not been taken into consideration in land–surface models representing global fluxes of water, in interpreting plant hydraulic status or in the determination of species' vulnerability to drought. A key trait required to represent foliar uptake at canopy to ecosystem scales is conductance to foliar uptake, K_{FWU}, which is the flux of water into the leaf normalised by the water potential difference between the leaf and water source. This trait is biophysically equivalent to stomatal conductance, g_s; however, the two variables are typically normalised by different measures of water 'concentration'. Here we show that when converted to the same units, the typical ranges of g_s overlap with the few published values of K_{FWU} suggesting that, theoretically, water vapour moving in through the stomata could partially, or even wholly, account for the fluxes attributed to foliar water uptake in some species. Establishing the extent to which such 'reverse transpiration' contributes to foliar uptake may be key to incorporating foliar water uptake into our existing understanding of plant-atmosphere interactions.

Key words

Reverse transpiration, vapour exchange, unsaturation, water relations, water cycle, drought, plant hydraulics

Opinion

There is a consensus emerging that foliar water uptake (FWU) may be the norm rather than the exception in plants globally (Berry, Emery, Gotsch, & Goldsmith, 2019), and that it may influence our understanding of how plants are coupled with the physical environment. Evidence suggests that FWU may result in significant fluxes of water at the ecosystem scale (Binks et al. 2019), and could play a fundamental role in determining the hydraulic vulnerability of plants both in terms of partially decoupling canopies from the soil water status (Binks et al., 2019; Schreel & Steppe, 2019; Simonin, Santiago, & Dawson, 2009) and of the potential of branch-level uptake to refill embolised conduits (Mayr et al., 2014). The mechanism of water ingress into leaves is of wide interest and various pathways have been proposed. These include water movement directly through the cuticle (Goldsmith, Matzke, & Dawson, 2013), either through pores (Schonherr, 2006), abrasion-related cracks (Hoad, Jeffree, & Grace, 1992), or adsorption onto, and transport through, the cuticular matrix (Schönherr & Schmidt, 1979); water movement through specialised structures such as trichomes (C. B. Eller, Lima, & Oliveira, 2016; Nguyen, Meir, Wolfe, Mencuccini, & Ball, 2016) or hydathodes (Martin & von Willert, 2000); and pathways for liquid water moving through stomata (Berry, White, & Smith, 2014; Burkhardt, Basi, Pariyar, & Hunsche, 2012).

In order to quantify the impact and magnitude of water taken up via FWU it is necessary to determine the conductance to FWU, K_{FWU} (g m^{-2} MPa^{-1} s^{-1}) which, defined using the Ohm's law analogy (van den Honert, 1948), is the flux into the leaf normalised by the water potential difference between the source and the leaf.

$$K_{fu} = \frac{dM}{dt\ A\ \Delta\Psi} = \frac{F}{\Delta\Psi} \quad (1)$$

Where dM is the net water exchange between the leaf and atmosphere or surface water (g), A is leaf area (m^2), dt is time elapsed (s), $\Delta\Psi$ is the difference in water potential between the surface water and the leaf (MPa), and F is the flux (g m^{-2} s^{-1}). A 'flux' here is defined as the net exchange of water over time normalised by cross sectional area and, while in the context of FWU it is water moving into the leaf from the external environment, we use the term to include transpiration in which the flux occurs in the opposite direction, where transpiration is positive and FWU is negative. K_{FWU} is required to estimate the total amount of water taken into the leaves over time and how foliar water uptake may change in response to changing climate. To date, however, only two publications have measured and reported this value: Guzman-Delgado et al. (2018) reported values of 0.084 mmol m^{-2} s^{-1} MPa^{-1} for *Prunis dulcis* and 0.021 mmol m^{-2} s^{-1} MPa^{-1} for *Quercus lobata*, while Binks et al. (2019) reported 0.122 mmol m^{-2} s^{-1} MPa^{-1} as an average for six common Amazonian tree genera.

In this *Opinion* we aim to show that the magnitude of the K_{FWU} values reported above are consistent with the diffusion of vapour into stomata under commonly occurring environmental conditions. Thus, we introduce the possibility that FWU could be partly, or even wholly, accounted for by vapour uptake in some species. The potential for this vapour flux into the leaf has been proposed previously and was intuitively referred to as 'reverse transpiration' (Vesala et al., 2017) which is the terminology we adopt here.

K_{FWU} can be considered as fundamentally the same biophysical property as stomatal conductance: the flux of water between the leaf and the atmosphere normalised by a difference of water 'concentration'. For the derivation of stomatal conductance, g_s, the concentration of water vapour is expressed in the dimensionless units of mole fraction vapour pressure deficit, therefore giving g_s the same units as transpiration, E, mmol m^{-2} s^{-1}. Thus,

74 the equation for g_s, assuming that boundary layer conductance is non-limiting and that there
75 is a negligible difference between leaf and air temperature (Nobel, 1999), is:

76 $$g_s = \frac{E}{D} = E\frac{P_a}{VPD} \quad (2)$$

77 Where D is the mole fraction vapour pressure deficit (unitless), P_a is air pressure (kPa) and
78 VPD is vapour pressure deficit (kPa). For measurements of stomatal conductance, the
79 humidity in the leaf air spaces is always assumed to be at 100 % relative humidity (RH) and
80 thus VPD = SVP (100 – RH_{air}) / 100, where SVP is saturation vapour pressure (kPa). In fact,
81 the humidity in leaves is not always 100 % but in equilibrium with the leaf water potential
82 (Vesala et al., 2017), this assumption is addressed quantitatively later on in the text.

83 Because relative humidity has a water potential equivalent (e.g. 100 % RH = 0 MPa, and 95
84 % RH = -6.8 MPa at 20 °C, Fig. 1), it is possible to express g_s in the same units as K_{FWU}
85 (becoming g_Ψ) by substituting D in equation 2 for the water potential of the air (Ψ_a) making
86 the two values directly comparable (see SI for discussion of the limitations of expressing
87 humidity as water potential):

88 $$g_\Psi = \frac{E}{\Psi_a} \quad (3)$$

89 Where Ψ_a is derived by (Pickard, 1981; Spanner, 1951):

90 $$\Psi_a = \frac{RT\ ln(RH/100)}{V_w \cdot 10^6} \quad (4)$$

91 R is the universal gas constant (8.13 J mol^{-1} K^{-1}), T is the temperature (K), V_w is the molar
92 volume of liquid water ($1.80x10^{-5}$ m^3 mol^{-1}), and 10^6 is a conversion factor to express units in

MPa. Thus, by combining equations 2-4, we can convert the units of g_s to normalise by water potential difference (g_ψ, mmol m^{-2} s^{-1} MPa^{-1}):

$$g_\psi = -g_s \frac{VPD\ V_w \cdot 10^6}{P_a\ RT\ ln(RH/100)} \quad (5)$$

In a recent meta-analysis, Hoshika et al. (2018) found that g_{max} ranged from 70 to 360 mmol m^{-2} s^{-1} in woody plants and up to 610 mmol m^{-2} s^{-1} in crop plants which is equivalent to g_ψ values of 0.010, 0.053 and 0.090 mmol m^{-2} s^{-1} MPa^{-1}, respectively (assuming g_s values measured at an average of 20 ºC and 70 % RH, see SI for sensitivity analysis). This range overlaps with the reported values for K_{FWU} listed above, showing that the measured FWU could have been partially or wholly due to vapour uptake (i.e., -*E,* Fig 2).

As stated previously, standard measurements of stomatal conductance make the assumption that the internal air spaces in leaves are at saturated vapour pressure (Cernusak et al., 2018; Gaastra, 1959). Therefore, the diffusion gradient considered for g_s is the difference between the saturated vapour pressure at leaf temperature and the actual vapour pressure of the air. However, this assumption is seldom correct as leaf water potentials < 0 MPa result in equilibrium vapour pressures lower than saturation (Buckley & Sack, 2019; Vesala et al., 2017). Rearranging equation 4 to find RH for a given water potential shows that, at 20 ºC, a leaf water potential of -1 MPa leads to an equilibrium vapour pressure equivalent of 99.2 % RH. Therefore, while the assumption is rarely correct, it generally has a minor effect on the calculation of stomatal conductance under conditions that favour photosynthesis. Other evidence suggests that internal leaf humidity may occur as much as 10 to 20 % below saturation due to hydraulic limitations on liquid water movement through leaves (Cernusak et al., 2018). Under these conditions, when the leaf boundary layer is at saturated vapour

pressure, as it would be when the leaves are wet or when dew is forming, the vapour pressure gradient is reversed favouring vapour movement into the leaf: reverse transpiration.

In order for reverse transpiration to occur, the following three conditions must be met:

1. leaf water potential of < 0 MPa,
2. atmospheric humidity close to 100 % RH (as it would be when leaves are wet or dew is forming),
3. $g_s > 0$ mmol m^{-2} s^{-1}

Due to the effect of gravity on the water column in trees, coupled with hydraulic resistance in the xylem, leaf water potentials are usually significantly less than 0 MPa in the absence of foliar water uptake (Binks et al., 2019); hence, condition 1 of the 3 criteria above is very often met. In a study of 28 sites worldwide, Kim et al. (2010) show that leaves are wet for an average of 8.7 hour day^{-1}, during which time the leaf boundary layer humidity must be close to saturation, meaning that condition 2 is met on average for around 30 % of the time at the sampled sites. Finally, because of the methodological challenges to measuring stomatal conductance on wet leaves, few studies have measured this process. However, the effect of leaf wetting on g_s differs between species and has been variously reported to reduce, have no measureable effect on, or to increase stomatal conductance (Ishibashi & Terashima, 1995; Smith & McClean, 1989). Moreover, there is good evidence to suggest the widespread occurrence of positive g_s at night (Caird, Richards, & Donovan, 2007; de Dios et al., 2015). These factors together indicate that stomatal behaviour may vary outside the normal constraints of photosynthetic stomatal optimisation (Mencuccini, Manzoni, & Christoffersen, 2019), suggesting that g_s does not always equal zero while leaves are wet, and therefore condition 3 is also expected to be met at least some of the time. Therefore, it seems highly

likely that all three conditions will co-occur under natural conditions leading to the occurrence of reverse transpiration. Using the definition for K_{FWU} described in equation 1 it is possible to determine the amount of water vapour that could theoretically diffuse into stomata under given conditions (Fig 3).

There is some clear evidence, primarily from dye tracer experiments, for the existence of non-stomatal pathways for liquid water to move into leaves (Cleiton B. Eller, Lima, & Oliveira, 2013; Gouvra & Grammatikopoulos, 2003; Nguyen et al., 2016). Moreover, films of liquid water have been reported to connect apoplastic water inside the leaf with free water on the leaf surface, facilitated by the presence of certain solutes (Burkhardt, 2010; Eichert & Goldbach, 2008). It therefore appears likely that there are multiple pathways of water entry into leaves, and these are likely to vary among species (Berry et al., 2019). What is different about the stomatal pathway, if it occurs, is that it could be highly dynamic and this would need to be taken into account in the method for determining K_{FWU}. Consequently, establishing the proportion of FWU that is accounted for by reverse transpiration may help with future investigation into this topic, and ultimately being able to represent K_{FWU} accurately in land-atmosphere models. The occurrence of reverse transpiration could have a number of significant implications: principally that the flux is under stomatal control, and that evolutionary selection pressure may have acted on stomatal behaviour to increase the potential for water vapour uptake.

In conclusion, the purpose of this *Opinion* is to make researchers aware that - biophysically - g_s and K_{FWU} can be considered equivalent conductance terms. In order to determine the significance of FWU at canopy to global scales it is necessary to measure a term for K_{FWU}, but future research should also aim to determine if (and in what taxa and climate regimens) this pathway is fundamentally different to g_s. The finding that reverse transpiration

contributes significantly to foliar water uptake, and plant water status in general, may provide a fast-track route to the incorporation of atmosphere-leaf-atmosphere water fluxes into our existing understanding and models of plant-environment water relations.

References

Berry, Z. C., Emery, N. C., Gotsch, S. G., & Goldsmith, G. R. (2019). Foliar water uptake: Processes, pathways, and integration into plant water budgets. *Plant, cell & environment, 42*(2), 410-423. doi:10.1111/pce.13439

Berry, Z. C., White, J. C., & Smith, W. K. (2014). Foliar uptake, carbon fluxes and water status are affected by the timing of daily fog in saplings from a threatened cloud forest. *Tree physiology, 34*(5), 459-470. doi:10.1093/treephys/tpu032

Binks, O., Mencuccini, M., Rowland, L., da Costa, A. C. L., de Carvalho, C. J. R., Bittencourt, P., . . . Meir, P. (2019). Foliar water uptake in Amazonian trees: evidence and consequences. *Global Change Biology, 0*(ja). doi:10.1111/gcb.14666

Buckley, T. N., & Sack, L. (2019). The humidity inside leaves and why you should care: implications of unsaturation of leaf intercellular airspaces. *Am J Bot, 106*(5), 618-621. doi:10.1002/ajb2.1282

Burkhardt, J. (2010). Hygroscopic particles on leaves: nutrients or desiccants? *Ecological monographs, 80*(3), 369-399. doi:10.1890/09-1988.1

Burkhardt, J., Basi, S., Pariyar, S., & Hunsche, M. (2012). Stomatal penetration by aqueous solutions – an update involving leaf surface particles. *New Phytologist, 196*(3), 774-787. doi:doi:10.1111/j.1469-8137.2012.04307.x

Caird, M. A., Richards, J. H., & Donovan, L. A. (2007). Nighttime Stomatal Conductance and Transpiration in C3 and C4 Plants. *Plant Physiology, 143*(1), 4. doi:10.1104/pp.106.092940

Cernusak, L. A., Ubierna, N., Jenkins, M. W., Garrity, S. R., Rahn, T., Powers, H. H., . . . Farquhar, G. D. (2018). Unsaturation of vapour pressure inside leaves of two conifer species. *Scientific Reports, 8*(1), 7667. doi:10.1038/s41598-018-25838-2

Dawson, T. E., & Goldsmith, G. R. (2018). The value of wet leaves. *The New phytologist, 219*(4), 1156-1169. doi:10.1111/nph.15307

de Dios, V. R., Roy, J., Ferrio, J. P., Alday, J. G., Landais, D., Milcu, A., & Gessler, A. (2015). Processes driving nocturnal transpiration and implications for estimating land evapotranspiration. *Scientific Reports, 5*, 10975. doi:10.1038/srep10975

Eichert, T., & Goldbach, H. E. (2008). Equivalent pore radii of hydrophilic foliar uptake routes in stomatous and astomatous leaf surfaces--further evidence for a stomatal pathway. *Physiologia plantarum, 132*(4), 491-502. doi:10.1111/j.1399-3054.2007.01023.x

198 Eller, C. B., Lima, A. L., & Oliveira, R. S. (2013). Foliar uptake of fog water and transport
199 belowground alleviates drought effects in the cloud forest tree species, Drimys
200 brasiliensis (Winteraceae). *The New phytologist, 199*(1), 151-162.
201 doi:10.1111/nph.12248

202 Eller, C. B., Lima, A. L., & Oliveira, R. S. (2016). Cloud forest trees with higher foliar water
203 uptake capacity and anisohydric behavior are more vulnerable to drought and climate
204 change. *The New phytologist, 211*(2), 489-501. doi:10.1111/nph.13952

205 Gaastra, P. (1959). *Photosynthesis of crop plants as influenced by light, carbon dioxide,*
206 *temperature, and stomatal diffusion resistance.* Veenman, Wageningen. Retrieved
207 from http://edepot.wur.nl/183268

208 Goldsmith, G. R., Matzke, N. J., & Dawson, T. E. (2013). The incidence and implications of
209 clouds for cloud forest plant water relations. *Ecology Letters, 16*(3), 307-314.
210 doi:doi:10.1111/ele.12039

211 Gouvra, E., & Grammatikopoulos, G. (2003). Beneficial effects of direct foliar water uptake
212 on shoot water potential of five chasmophytes. *Canadian Journal of Botany, 81*(12),
213 1278-1284. doi:10.1139/b03-108

214 Guzman-Delgado, P., Earles, J. M., & Zwieniecki, M. A. (2018). Insight into the
215 physiological role of water absorption via the leaf surface from a rehydration kinetics
216 perspective. *Plant Cell and Environment, 41*(8), 1886-1894. doi:10.1111/pce.13327

217 Hoad, S. P., Jeffree, C. E., & Grace, J. (1992). Effects of wind and abrasion on cuticular
218 integrity in Fagus sylvatica L. and consequences for transfer of pollutants through leaf
219 surfaces. *Agriculture, Ecosystems & Environment, 42*(3), 275-289.
220 doi:https://doi.org/10.1016/0167-8809(92)90004-U

221 Hoshika, Y., Osada, Y., de Marco, A., Peñuelas, J., & Paoletti, E. (2018). Global diurnal and
222 nocturnal parameters of stomatal conductance in woody plants and major crops.
223 *Global Ecology and Biogeography, 27*(2), 257-275. doi:10.1111/geb.12681

224 Ishibashi, M., & Terashima, I. (1995). Effects of continuous leaf wetness on photosynthesis:
225 adverse aspects of rainfall. *Plant, Cell & Environment, 18*(4), 431-438.
226 doi:10.1111/j.1365-3040.1995.tb00377.x

227 Kim, K. S., Taylor, S. E., Gleason, M. L., Nutter, F. W., Coop, L. B., Pfender, W. F., . . .
228 Orlandini, S. (2010). Spatial portability of numerical models of leaf wetness duration
229 based on empirical approaches. *Agricultural and Forest Meteorology, 150*(7), 871-
230 880. doi:https://doi.org/10.1016/j.agrformet.2010.02.006

231 Martin, C. E., & von Willert, D. J. (2000). Leaf Epidermal Hydathodes and the
232 Ecophysiological Consequences of Foliar Water Uptake in Species of Crassula from
233 the Namib Desert in Southern Africa. *Plant Biology, 2*(2), 229-242. doi:10.1055/s-
234 2000-9163

235 Mayr, S., Schmid, P., Laur, J., Rosner, S., Charra-Vaskou, K., Dämon, B., & Hacke, U. G.
236 (2014). Uptake of Water via Branches Helps Timberline Conifers Refill Embolized
237 Xylem in Late Winter. *Plant Physiology, 164*(4), 1731-1740.
238 doi:10.1104/pp.114.236646

239 Mencuccini, M., Manzoni, S., & Christoffersen, B. (2019). Modelling water fluxes in plants:
240 from tissues to biosphere. *New Phytologist, 222*(3), 1207-1222.
241 doi:10.1111/nph.15681

242 Nguyen, H. T., Meir, P., Wolfe, J., Mencuccini, M., & Ball, M. C. (2016). Plumbing the
243 depths: extracellular water storage in specialized leaf structures and its functional
244 expression in a three-domain pressure -volume relationship. *Plant, cell &*
245 *environment, 40*(7), 1021-1038. doi:10.1111/pce.12788

246 Nobel, P. S. (1999). *Physicochemical and environmental plant physiology*: Elsevier
247 Academic Press.

248 Pickard, W. F. (1981). THE ASCENT OF SAP IN PLANTS. *Progress in Biophysics &*
249 *Molecular Biology, 37*(3), 181-229.

250 Schonherr, J. (2006). Characterization of aqueous pores in plant cuticles and permeation of
251 ionic solutes. *Journal of experimental botany, 57*(11), 2471-2491.
252 doi:10.1093/jxb/erj217

253 Schönherr, J., & Schmidt, H. W. (1979). Water permeability of plant cuticles. *Planta, 144*(4),
254 391-400. doi:10.1007/BF00391583

255 Schreel, J. D. M., & Steppe, K. (2019). Foliar water uptake changes the world of tree
256 hydraulics. *npj Climate and Atmospheric Science, 2*(1), 1. doi:10.1038/s41612-018-
257 0060-6

258 Simonin, K. A., Santiago, L. S., & Dawson, T. E. (2009). Fog interception by Sequoia
259 sempervirens (D. Don) crowns decouples physiology from soil water deficit. *Plant,*
260 *cell & environment, 32*(7), 882-892. doi:10.1111/j.1365-3040.2009.01967.x

261 Smith, W. K., & McClean, T. M. (1989). Adaptive Relationship Between Leaf Water
262 Repellency, Stomatal Distribution, and Gas Exchange. *American Journal of Botany,*
263 *76*(3), 465-469. doi:10.2307/2444617

264 Spanner, D. C. (1951). The Peltier Effect and its Use in the Measurement of Suction Pressure.
265 *Journal of Experimental Botany, 2*(5), 145-168.

266 van den Honert, T. H. (1948). Water transport in plants as a catenary process. *Discussions of*
267 *the Faraday Society, 3*(0), 146-153. doi:10.1039/DF9480300146

268 Vesala, T., Sevanto, S., Gronholm, T., Salmon, Y., Nikinmaa, E., Hari, P., & Holtta, T.
269 (2017). Effect of Leaf Water Potential on Internal Humidity and CO2 Dissolution:
270 Reverse Transpiration and Improved Water Use Efficiency under Negative Pressure.
271 *Front Plant Sci, 8*, 54. doi:10.3389/fpls.2017.00054

272

273

Funding acknowledgements

ARC grant number to PM: FT110100457

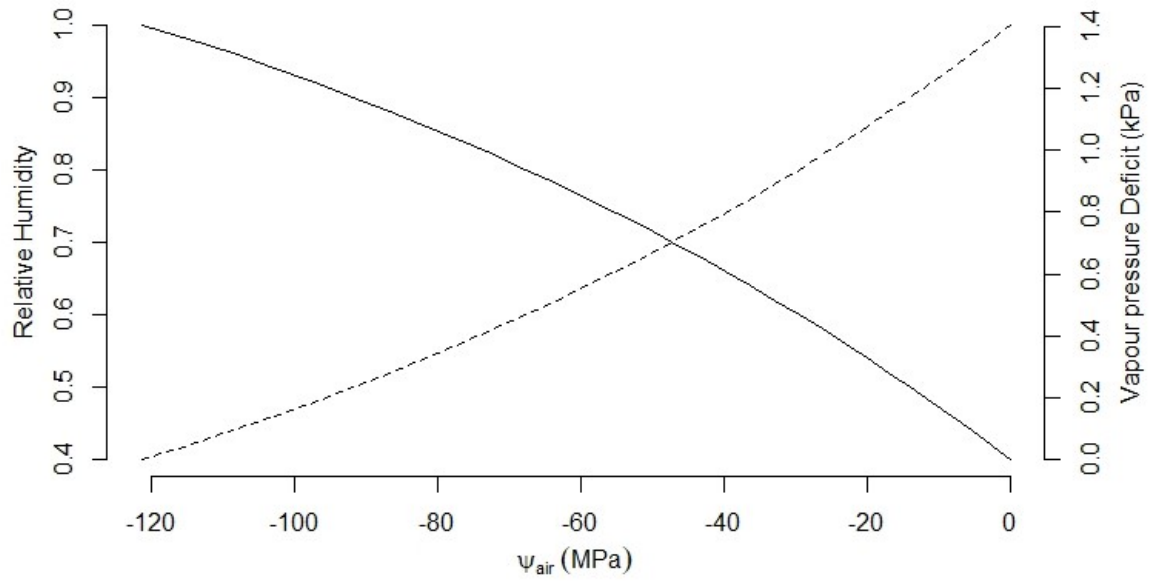
NERC grant numbers to PM: NE/K01627X/1 and NERC NE/L007924/1.

Figure legends

Figure 1. The equivalence between relative humidity (dashed line), vapour pressure deficit (VPD, solid line) and water potential.

Figure 2. The relationship between water vapour flux between the leaf and atmosphere (E) at different leaf and atmospheric water contents. The three x-axes show different ways to express the difference in water content/concentration of the leaf and atmosphere. The first axis represents the difference in 'relative deficit' between the leaf and the air, where RD is 1-(relative humidity / 100). The second axis is the difference between air and leaf water potential, where air vapour pressure is expressed as its water potential equivalent. The third axis is the vapour pressure difference between the air and the leaf, which is equivalent to vapour pressure deficit, taking into account that VPD in the internal air spaces of the leaf is > 0. The inset graph shows the detail of the shaded region in which the flux becomes negative (i.e. water vapour goes into the leaf, $-E$) over different leaf water potentials assuming that the RH_{air} = 100 %. The different lines show representative values for stomatal conductance where the dotted line is g_s = 100 mmol m^{-2} s^{-1}, the solid line is g_s = 350 mmol m^{-2} s^{-1} and the dot dash line is g_s = 600 mmol m^{-2} s^{-1}.

Figure 3. Relationship between the amount of water vapour diffusing into leaves, the duration of leaf wetness (or 100 % atmospheric humidity) and stomatal conductance (g_s), given a mean leaf water potential of -0.5 MPa. This figure combines the outcomes of equations 1 and 5 demonstrating the effect of stomatal conductance on water vapour uptake.

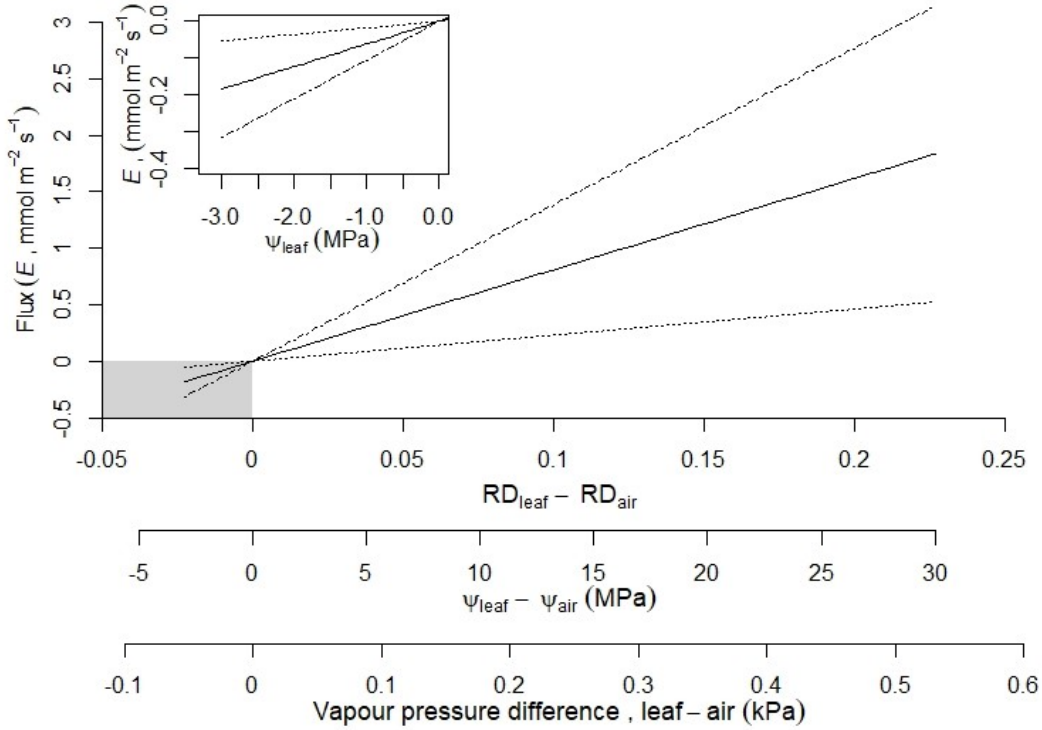


301

302 **Figure 1.** The equivalence between relative humidity (dashed line), vapour pressure deficit

303 (solid line) and water potential.

304



305

306 **Figure 2.** The relationship between water vapour flux between the leaf and atmosphere at
307 different leaf and atmospheric water contents. The three x-axes show different ways to
308 express the difference in water content/concentration of the leaf and atmosphere. The first
309 axis represents the difference in 'relative deficit' between the leaf and the air, where RD is 1-
310 RH (relative humidity). The second axis is the difference between leaf and air water
311 potential, where air vapour pressure is expressed as its water potential equivalent. The third
312 axis is the vapour pressure difference between the leaf and the air which is equivalent to
313 vapour pressure deficit, taking into account that VPD in the internal air spaces of the leaf is >
314 0. The inset graph shows the detail of the shaded region in which the flux becomes negative
315 (i.e. water vapour goes into the leaf) over different leaf water potentials assuming that the
316 RH_{air} = 100 %. The different lines show representative values for stomatal conductance
317 where the dotted line is g_s = 100 mmol m^{-2} s^{-1}, the solid line is g_s = 350 mmol m^{-2} s^{-1} and the
318 dot dash line is g_s = 600 mmol m^{-2} s^{-1}.

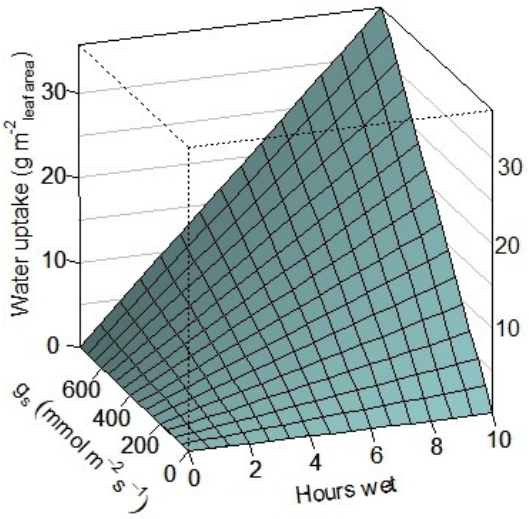


Figure 3. Relationship between the amount of water vapour diffusing into leaves, the duration of leaf wetness (or 100 % atmospheric humidity) and stomatal conductance (g_s), given a mean leaf water potential of -0.5 MPa.

Equivalence of foliar water uptake and stomatal conductance?

Supplementary Information

The sensitivity of g_ψ to temperature and humidity

Stomatal conductance is the flux of water vapour (transpiration) normalised by the gradient down which water vapour moves. The purpose of the normalisation is to get a physiologically meaningful measure that is independent of environmental conditions. However, because the relationship between saturated vapour pressure and air temperature is highly non-linear, it is not possible to express stomatal conductance in a way that completely negates the effect of the temperature and humidity at which the measurement was taken. There are a number of different ways to represent the concentration of water vapour in air including partial pressure (of vapour), mole fraction, relative humidity and water potential. Of these, mole fraction (vapour pressure deficit) was chosen to normalise the transpiration flux because the temperature dependence was least and differences in air pressure have no effect at all, in contrast to the other measures {Nobel}.

In the main paper we have used water potential of the air, Ψ_{air}, to normalise the flux so that transpiration can be interpreted in units consistent with plant hydraulics. However, Ψ_{air}, is more sensitive to the conditions under which it is measured than mole fraction VPD. Therefore, we had to assume values of humidity and temperature that represent the mean conditions under which the original measures of stomatal conductance were taken in order to convert them into g_ψ. The values of stomatal conductance in the main text were taken from a

meta-analysis by Hoshika et al. {Hoshika 2018} who selected data from 235 publications on the basis that the "data were obtained from field measurements to represent actual field conditions". We therefore chose the values of 20 ºC and 70 % relative humidity to convert the values of g_s to g_ψ.

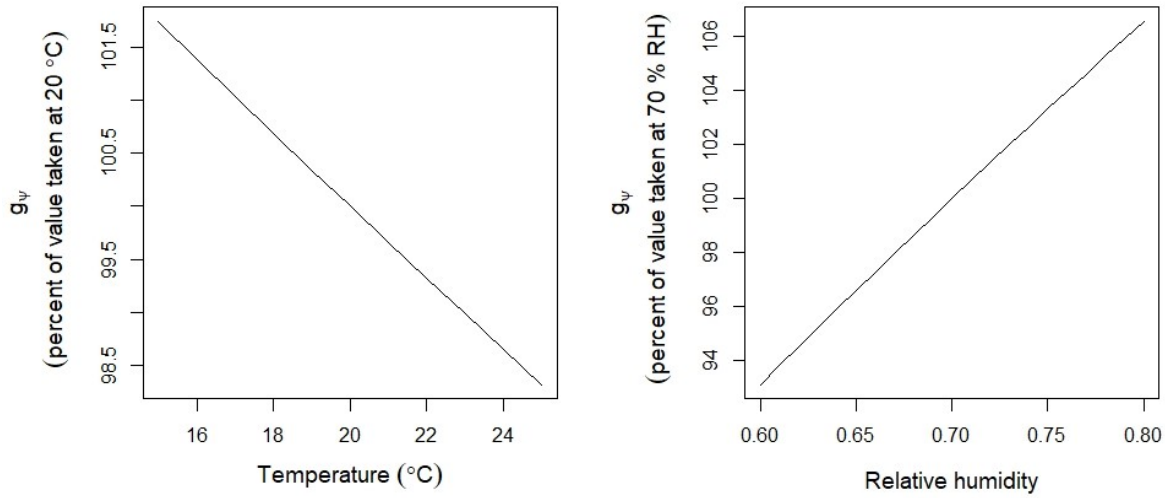


Figure S1. Sensitivity of the conversion of g_s to g_ψ on temperature (left) and relative humidity (right). g_ψ is expressed as a percentage of the value at 70 % relative humidity and 20 ºC on the y axes to enable an easy conversion of the figures presented in the main text to those derived from alternative values of temperature and humidity.